

capture prey. This strategy may be more energy efficient and effective in competing with the ants and other birds for the same food resource. In contrast, barred woodcreepers apparently prefer to forage from higher substrates. They utilize their climbing ability to capture insect prey that have moved up tree trunks, where they would be inaccessible to bicolored antbirds and gray-headed tanagers. Although tawny-winged woodcreepers foraged on trunks as well, barred woodcreepers dominated the higher vertical positions, perhaps excluding the tawny-winged woodcreepers from these heights by virtue of their greater body size.

The similarity of prey capture rates for all species suggest that direct competition does not limit foraging success in this community. The majority of prey captures were approximately equal to the bill length of the bird, so bird species that differ in bill size apparently differ in prey size selection. These results suggest that the birds have partitioned the resources provided by army ants through differences in both spatial distribution and prey selection.

Although the position of resources change rapidly with the movement of the army ant swarm, ant bird community structure is maintained. Because all species are comparable competitors, we would predict that larger swarms would support a greater number of individuals in the same relative proportions.

Resource bases that move in space are not unique to army ant communities. Other bird communities, such as frugivorous altitudinal migrants, are also challenged to continually readjust their position in response to the changing spatial patterns of fruiting trees. Similarly, mobile resources are also common in other systems, such as piscivores feeding on mobile schooling fish and large terrestrial predators that follow migrating ungulate communities across savannas. If these communi-

ties are like the antbirds, then they retain their structure of niche partitioning even as they and their resources move. This partitioning presumably allows them to harvest their resource base more completely and efficiently than if the organization of the community were continually disrupted by the movement of resources.

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SAME BAT-CHANNEL, SAME BAT TIME? THE EFFECTS OF TIME AND TIDE ON FORAGING BEHAVIOR OF THE PISCIVOROUS BULLDOG BAT

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Abstract: Community interactions in estuaries can result in unique adaptations and relationships between freshwater and marine species. Piscivorous bats (*Noctilio leporinus*) in the Rio Sirena lagoon of Corcovado National Park, Costa Rica may have evolved foraging schedules that differ from those of freshwater conspecifics by incorporating tidal cycles. Our data, combined with theses of Yale et al. (1998), indicate strong independent effects of both tide and time of night on bat foraging activity. In both years, there was a peak in bat foraging before dawn, which is apparently due to preparation for the upcoming day's fast. Also, in both years there was a peak in foraging activity that corresponded with high tide. We hypothesize that this is because the large marine fish and sharks that enter the lagoon at high tide drive the smaller fish on which *N. leporinus* feeds to the shallow water where they are easier to catch. To our knowledge, this is the first published report of tidal rhythms of any kind in any species of bat. Furthermore, these interactions suggest a previously undescribed commensalism between large marine fish and piscivorous bats and indicate that estuary systems such as the Sirena lagoon may be important for the regional abundance of *N. leporinus*.

Key Words: estuary, foraging, *Noctilio leporinus*, piscivory, tidal flux

INTRODUCTION

The Rio Sirena lagoon in Corcovado National Park, Costa Rica supports a population of *Noctilio leporinus*, the piscivorous greater bulldog bat. Found in Pacific coast lowlands of Central and South America, this species feeds on small fish (Emmons 1997). They use echolocation to locate surface ripples caused by fish activity, and then skim the water surface in an attempt to snag fish with their scimitar-shaped claws (Brandon 1983).

Kalko et al. (1998) found that freshwater piscivorous bats forage most at dusk and dawn, perhaps to recover from their last day's fast and to prepare for the next. In tidal environments, however, such as the Sirena lagoon in Corcovado National Park, *N. leporinus* must deal with periodic changes in water turbulence, fish behavior, and the composition of the fish community, all of which could effect foraging. Yale et al. (1998) found that the foraging activity of *N. leporinus* in the Sirena lagoon peaked at high tide and just before dawn. However, these observations were restricted to only two nights with high tides near 21:00

and 22:00. When we were at Corcovado, in February 2000, Sirena lagoon still supported a population of *N. leporinus*, but high tide was 6 hours later than in the 1998 study. We designed a study to further distinguish between two possible patterns in the foraging rhythms of this estuarine population of *N. leporinus*. Foraging rates may be chiefly influenced by the fasting cycles of bats, in which case bats should fish most at dusk and dawn. Alternatively, bat foraging may be influenced by prey availability, which may peak at high tide when large marine fish crowd small estuary fish into the shallow water preferred by foraging bats (Yale et al. 1998).

METHODS

This study was conducted in the Rio Sirena lagoon, Corcovado National Park, Costa Rica from dusk (18:00) to dawn (06:00) on three consecutive nights, beginning 4 February 2000. We divided the lagoon into 6 adjoining 35 m sections of shoreline (Fig. 1). We then monitored bat behavior in each section during 5 min intervals within 30 min obser-

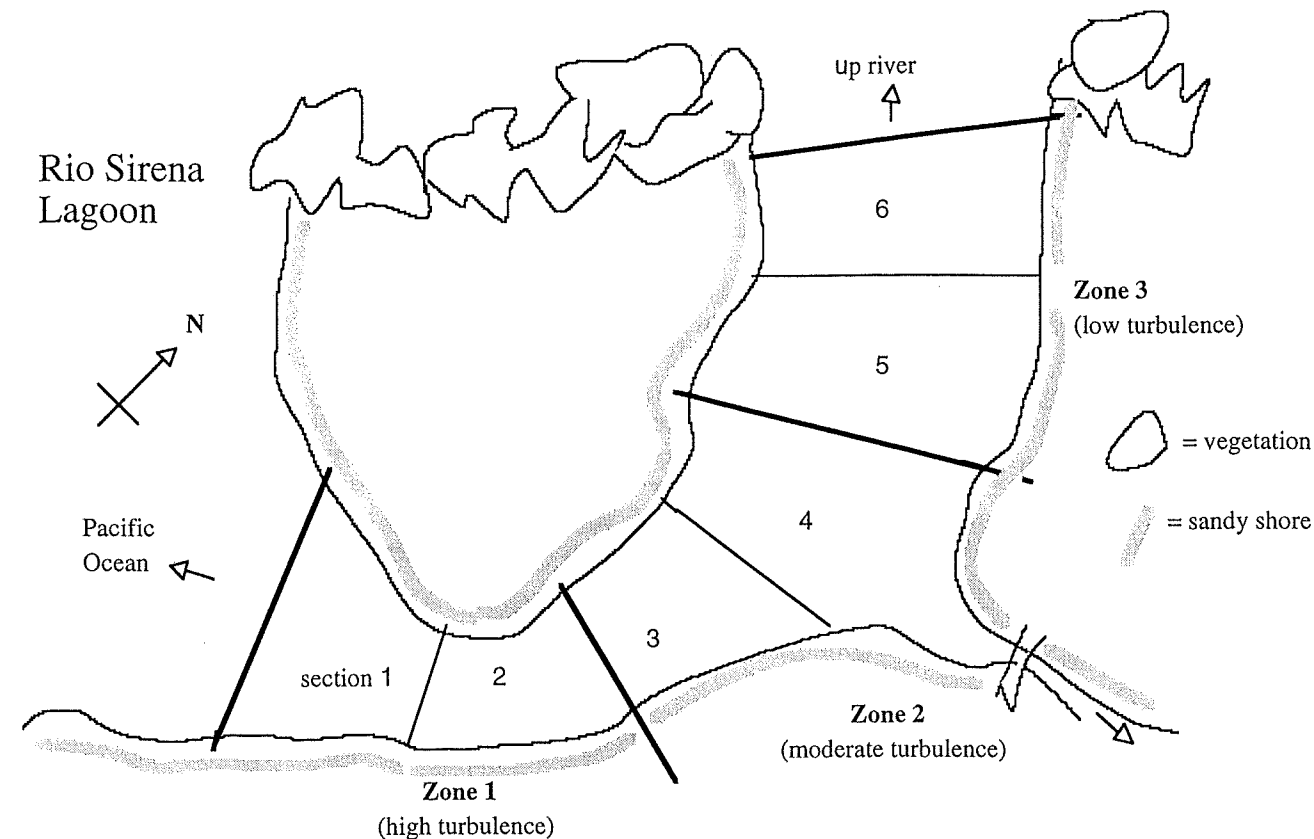


Figure 1. Map of the Rio Sirena Lagoon in Corcovado National Park, Costa Rica. Activity of bats and fish was recorded within each of 6 sampling sections of lagoon, constituting three zones of varying turbulence.

vation periods falling every 1 h 15 min, between 18:00 and 06:00 the following day. During each interval, we recorded the number of bat flights (each time a bat flew through an imaginary plane perpendicular to the plane of the water), bat fishing attempts (each time a bat contacted the water with its feet), and fish activity (audible and visual disturbances of the water surface by fish; Yale et al. 1998).

We estimated tidal variation in small fish density both at night and during the day. During each nocturnal observation interval, we counted all fish in five haphazardly chosen 15 x 15 cm plots located within 2 m of shoreline of each section. During the day, we counted all small fish entering or occupying two haphazardly chosen 1 x 1 m plots per section during 3 min. We estimated the minimum total population size of *N. leporinus* as the maximum number of individuals observed at any time during the three nights of

observations. We also searched for population roosting sites along the northeast edge of the lagoon, which is where bats flew from at dusk and flew towards at dawn.

We developed sinusoidal curves to express time and tide in units appropriate for regression analyses to test hypothesized patterns in bat foraging (Appendix 1). We used a stepwise regression approach to compare regression models that predicted bat foraging activity (fishing attempts) with different possible combinations of time, tide, and the interaction between time and tide. The set of possible independent variables also included second order polynomials (time² and tide²) to allow for nonlinearities in the effects of time and tide. Bat fishing attempts were normalized before regression analysis with a common log transformation.

The effects of fish jumps and small fish counts on bat fishing attempts (log trans-

formed) were analyzed with simple linear regressions. Daytime small fish counts were analyzed for effect of tide by one-way analysis of variance. To analyze the effect of turbulence on bat activity, study sections were separated into three zones of different exposure to wave action due to tide: Zone 1 (sect. 1 & 2) = high turbulence; Zone 2 (sect. 3 & 4) = mid turbulence; Zone 3 (sect. 5 & 6) = low turbulence (Fig. 1). The effect of zone on bat fishing attempts (log transformed) was analyzed with a one-way analysis of variance.

RESULTS

On all three nights of sampling in 2000, both the number of flights and fishing attempts rose dramatically during high tide and peaked the hour before sunrise (Fig. 2). On February 4, when high tide was earliest and most temporally separated from dawn, the foraging increase was most gradual (Fig. 2). On February 5 and 6, the increase in foraging began at a later time, corresponding to the shift in high tide, and increased at a faster rate (Fig. 2). The peak in foraging around 21:00 seen in 1998 was absent from our data (Fig. 3).

The combined data from 1998 and 2000 indicated strong effects of tide on bat foraging activity. Together, these factors explained 51% of the temporal variation in bat foraging activity in the Rio Sirena lagoon (Table 1). We found that both time of night and tide had sig-

nificant effects on bat foraging activity, and together can be used to predict more than 50% of the variation in bat foraging activity in the Rio Sirena lagoon (Table 1). There was no relationship between fish jumps or small fish counts and bat fishing attempts ($r = 0.08$, $P = 0.27$, $r = 0.11$, $P = 0.16$; respectively). Tide had no effect on apparent small fish counts during the day ($F_{2,21} = 0.89$, $P = 0.43$), but the power of this test was quite low because there were few sample plots and most sample plots contained no fish during our brief observations.

Water turbulence increased with the tide ($r = 0.74$, $P < 0.0001$). Most bat fishing attempts occurred at an intermediate level of turbulence within zone 2 ($F_{2,177} = 7.83$, $P < 0.001$; Fig. 4). We observed a maximum of 10 *N. leporinus* at one time, indicating that the colony includes at least that many individuals. One tree with a deep hole in the trunk was identified as a potential roosting site. It is a large, double-trunked tree on the second small peninsula after the main lagoon and ≈ 15 m W of the boat landing (Fig. 1).

DISCUSSION

Our results support the conclusion of Yale et al. (1998) that both tidal flux and time of night influence foraging rates of *N. leporinus*. In 1998, bat flights and fishing attempts peaked slightly before high tide and just before dawn (Fig. 3). The second foraging peak was just before dawn on both nights

Table 1. Regression model describing effects of time and tide on bat fishing attempts. Time and tide were scaled as sine functions (Appendix 1).

Best Fit Model ($r^2 = 0.51$):			
Log(fishing attempts + 1) = 1.452 + 0.519(Sine Time) - 2.813(Sine Tide) + 1.138(Sine Tide) ²			
Term	Coefficient	T ^a statistic	P ^a
Intercept	1.452	1.27	0.2130
Sine Time	0.519	3.71	0.0007
Sine Tide	-2.813	-1.80	0.0792
(Sine Tide) ²	1.138	2.21	0.0331

^a Testing the null hypothesis that corresponding coefficient = 0.

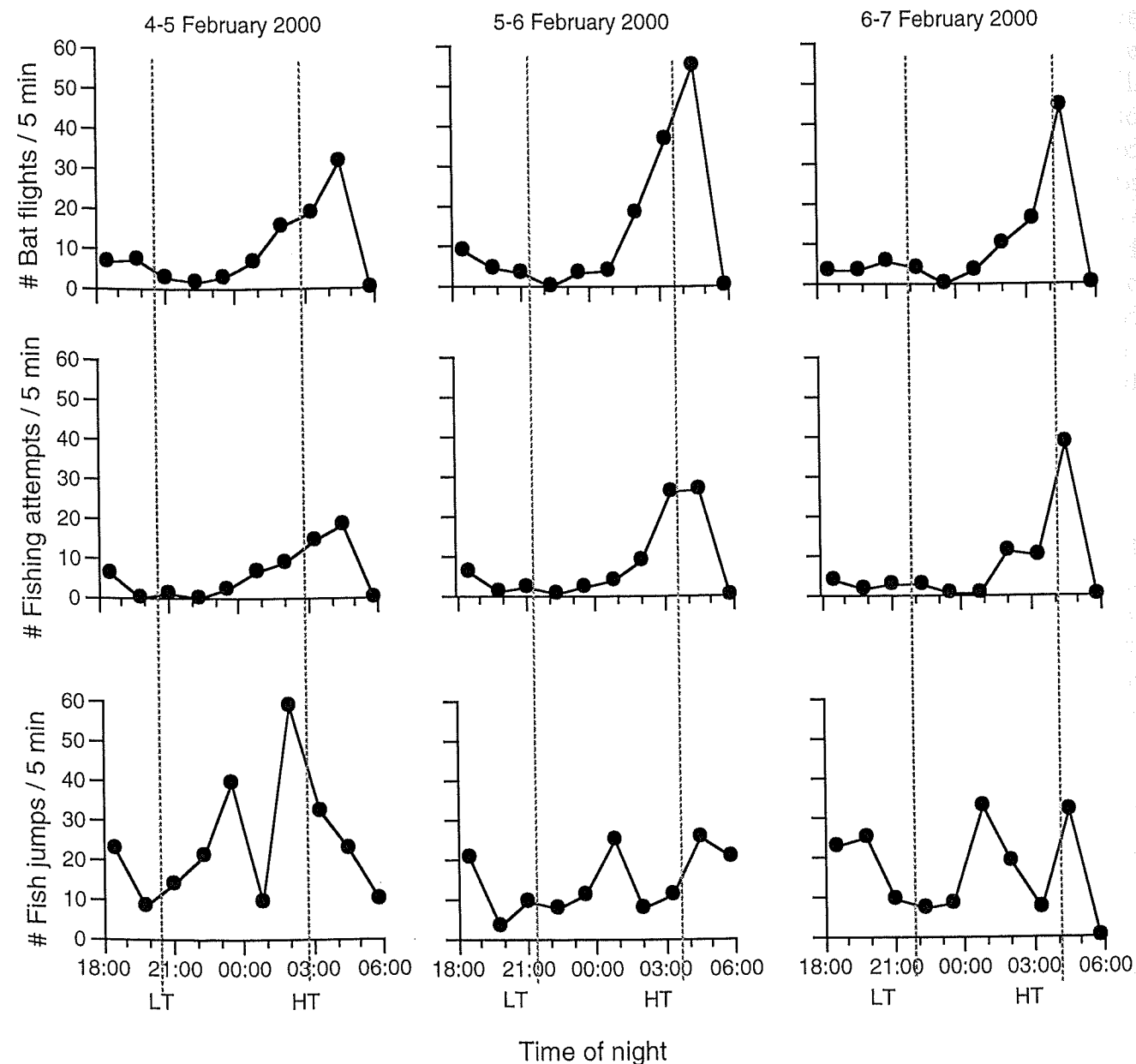


Figure 2. Number of bat flights, bat fishing attempts, and large fish jumps in 5 min sampling intervals within each of ten time periods, between 18:00 and 06:00 on three subsequent nights. High tides and low tides are indicated as HT and LT.

of the 1998 study, while the earlier peak shifted with the time of high tide. This shift suggested that tide influenced bat foraging, but with this data alone it was difficult to exclude the possibility that the first peak was associated with dusk and only coincidentally correlated with tide. However, foraging activity in 2000 also showed a conspicuous peak near the time of high tide even though high tide occurred \approx 6

hours later than in 1998. In 2000, high tide approached dawn, when foraging was absent in 1998; as it did, the period of foraging activity before daybreak became increasingly compressed (Fig. 3). The combined data from 1998 and 2000 provided strong evidence for independent effect of both time of night and tide for bat foraging rhythms. The regression model in Table 1 permits predictions of for-

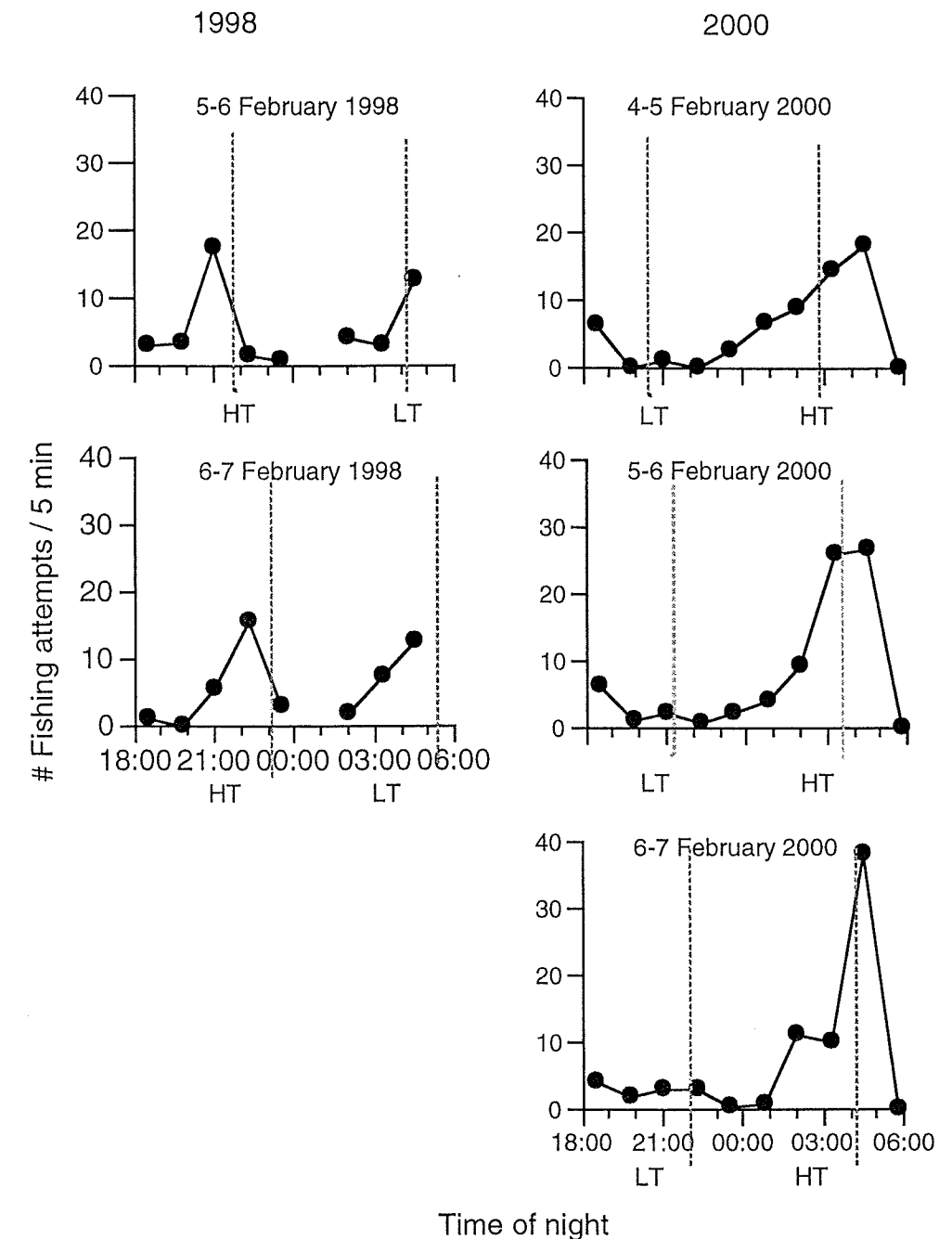


Figure 3. Number of bat flights in 5 min across ten time periods on two nights in 1998 and three in 2000. High tides and low tides are indicated as HT and LT.

aging rhythms under any phase of the tidal cycle.

Bats presumably forage at dawn to prepare for the impending daylong fast; this seems to be fixed behavior regardless of the tidal cycle. It is more surprising that the Rio Sirena bat population also has the behavioral

flexibility to track tidal cycles, as suggested by Yale et al. (1998). We observed shark fins and marine fish in the lagoon at high tide, suggesting that marine predators enter the lagoon as the tide rises. We hypothesize that the rise in marine predators causes an increase in bat prey availability by driving small fish

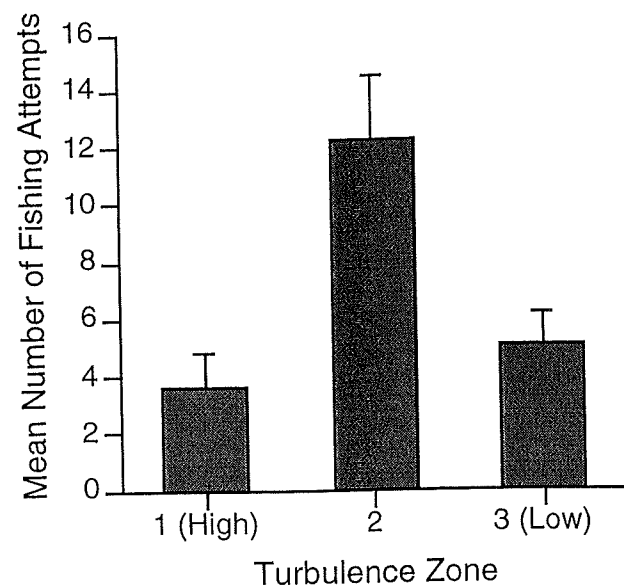


Figure 4. *N. leporinus* fishing attempts within each of 3 zones in the lagoon (Fig. 1). Zones were defined by water turbulence during tidal fluxes, with zone 1 being high turbulence and zone 3 being low turbulence.

to the shallow lagoon edge. As the small fish school and jump in attempt to escape, they may create surface ripples that bats can detect via echolocation. Furthermore, they should be easier to capture in shallow water, both because the fish are more concentrated, and because they cannot easily escape the reach of bat claws. The interaction between marine fish and sharks and bulldog bats suggests a commensalism that is previously undescribed. However, further studies of fish activity in the lagoon are required to verify this hypothesis, and in fact our measurements of fish abundance did not reveal the pattern that we hypothesize.

Bats seemed to prefer foraging in moderately turbulent water. Water turbulence changes with tidal flux and tends to be highest at the high tide. Other studies have indicated that piscivorous bats preferentially fish over calm water, where background turbulence that could interfere with echolocation is minimized (Brandon 1983). Brandon's study (1983), however, dealt with freshwater bats that could not have benefited from the in-

creased prey abundance associated with tidal turbulence. For the Rio Sirena population, high turbulence may still obscure prey ripples and make echolocation difficult, but moderately turbulent water with high concentrations of prey in shallow water may still afford more profitable foraging than the calmest water that is available in the lagoon. As water turbulence changes, bats may shift the location of their foraging within the lagoon to balance ease of echolocation with prey availability.

Estuaries that permit bats to exploit the effects of large marine predators may have high value for *N. leporinus*. Some *N. leporinus* were also observed foraging during February 2000 in the mouth of the nearby Rio Claro (≈ 2 km S of the Sirena lagoon), but a search in February 1998 failed to detect *N. leporinus* in the Rio Claro. The Rio Claro differs from the Sirena lagoon in that tidal fluxes produce much weaker effects on water depth and turbulence. Furthermore, there seems to be many fewer marine predators that enter the Rio Claro at high tide. The Sirena lagoon supports a stable population of *N. leporinus*, perhaps because the lagoon morphology facilitates marine predators that enhance bat foraging. It may be that estuaries such as the Sirena lagoon support source populations of *N. leporinus* that are important to landscape population dynamics.

Furthermore, such estuaries create the potential for strong community interactions that are somewhat surprising because they involve organisms such as bats and sharks that are not normally regarded as part of the same system.

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APPENDIX 1: FORMULAS TO CONVERT TIME AND TIDE TO SINUSOIDAL FUNCTIONS

SINE TIME (SCALED FROM 1 TO 2 WITH VALUES OF 2 ASSIGNED TO DUSK AND DAWN) =
 $[1 + \sin[\pi/2 + (\text{min after sunset of sampling time})(2\pi)/720 \text{ min of dark}]]/2$

SINE TIDE (SCALED FROM 1 TO 2 WITH VALUES OF 2 ASSIGNED TO HIGH TIDE) =
 $[1 + \sin[-\pi/2 + (\text{min after sunset of sampling time} - \text{min after sunset of low tide})(2\pi)/\text{min between low tides}]]/2$